

Virtual Experiments in Marine Bioacoustics: Whales, Fish, and Anthropogenic Sound

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LONG-TERM GOALS

This programmatic effort has three long-term goals. The **first** is to simulate bioacoustic interactions within and near individual fish. We developed a methodology that combines x-ray CT scans with tissue elasticity measurements and finite-element modeling software, the *vibroacoustic toolkit* (VATk). This technique has provided significant insights and discoveries regarding toothed whale bioacoustics (Cranford *et al.*, 2008b; Cranford *et al.*, 2008c), and now, within a fish's head. The **second** long-term goal is to improve and refine our ability to measure tissue elasticity in samples by building a portable device to measure physical properties from tissue samples so that these quantities can be incorporated into our models. The **third** and final goal is to validate the finite element models by comparing them to dolphin hearing results from psychoacoustic experiments. Accomplishing these goals has caused us to develop additional functionality to the VATk software.

OBJECTIVES

The **primary** objective is to examine simulations of fish otolith organs to elucidate patterns of motion in response to acoustic stimuli from different directions and of different frequencies. The **secondary** objective is to standardize and improve our ability to measure tissue properties; primarily bulk and

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shear modulus. The **tertiary** objective is to validate these finite element models and refine the vibroacoustic toolkit (VATk).

APPROACH

Fish Hearing: In teleost fishes there are three pairs of otoliths, dense masses or “stones” of calcium carbonate, each sitting upon a patch of hair cells, all contained within fluid filled sacs. We have generated high-resolution CT-scans of the White Seabass (*Atractoscion nobilis*) and segmented the otolith organs from the scanned volumes for image analysis.

Otolith organs (Popper *et al.*, 1988; Popper and Lu, 2000; Popper *et al.*, 2003; Popper *et al.*, 2005; Popper and Schilt, 2008) may allow fish to analyze sound frequency and direction, but the mechanism(s) remains elusive. It is necessary to account for the ability of fish to discriminate sounds of differing frequency, reviewed by Enger (1973). Sand has suggested that the movement patterns of the otoliths may be frequency dependent, and that the parts of the macula which are stimulated may depend upon frequency (Sand, 1974). Further studies are necessary before this notion can be confirmed or refuted.

Fish can determine the direction of a sound source (see review by Sand and colleagues) (Sand and Karlsen, 1986; Sand and Bleckmann, 2007). One obstacle to understanding the mechanisms for these capacities is our lack of knowledge about the movements of the otoliths themselves. For example, *do otoliths show simple translation back and forth along the axis of sound wave propagation or are the motions more complex?* Horner (1980) suggested that the saccular otolith can only rock within the fluid-filled sacs and upon the macula because of constraints from proximal structures and fibrous attachments within the ear.

In order to determine the effect that otolith shape might have on otolith motion, we ran two sets of simulations using our numerical analysis software. In the first simulations (Extracted Otoliths Simulations), we extracted the shapes of all six otoliths from high-resolution microCT scans of the White Seabass. Those “otoliths” were assigned uniform calcareous material properties, immersed in a simulated shear-soft jelly, and exposed to different stimulus frequencies from different directions.

In the second set of simulations (Simplified Otolith Simulations), we compared the responses of simplified otolith-like shapes with the results of the Extracted Otoliths Simulations. In this second simulation, we used two simple shapes, a “spherical otolith” and a “hemispherical otolith.”

Tissue Elasticity Measurement: Our first attempts to develop a device to measure tissue elasticity were unsuccessful. We have now developed an alternative methodology, modifying a device known as the Linear Skin Rheometer (LSR) as the central component (Hess *et al.*, 2006). The engineering design also calls for a companion component that will allow us to measure sound speed in the tissue samples.

Model Validation and Dolphin Hearing: One crucial step in building a finite element model is a process called *validation*. This process tests the veracity of the model by comparing virtual simulations to actual experimental results for dolphin hearing.

WORK COMPLETED

Fish Hearing: We have completed the two elementary otoliths models (Extracted Otoliths Simulations and Simplified Otolith Simulations) and can report that the otoliths rock in response to planar harmonic waves from different directions and stimulus frequencies. We have published one paper on the Simplified Otolith Simulations (Krysl *et al.*, 2012) and have produced a manuscript that reports on the Extracted Otoliths Simulations. This manuscript is now in revision.

Tissue Elasticity Measurement: The linear skin rheometer concept is being refined into a prototype device. The sample will be located between two plates. The bottom plate is used for support; the top plate has a circular opening that exposes a limited extent of the surface. Force is applied to the exposed surface and the resulting displacement and its phase shift are measured in a certain frequency range. The resulting physical setup is amenable to modeling as the boundary conditions can be estimated with confidence. Also, the sample need not be extracted with high precision.

Model Validation and Dolphin Hearing: The psychoacoustic measurements of the head-related transfer function (HRTF) with a live bottlenose dolphin have been completed by Dr. Paul Nachtigall and his colleagues at Cocoanut Island, Hawaii. Unfortunately, we cannot report those findings here because we want to remain “blind” to the results until we calculate the HRTF sound field with our finite element model. This process has been delayed while we locate an appropriately fresh dead specimen with which to build the model.

A procedure for extrapolating the scattered or total harmonic pressure in the near field using the Helmholtz integral was implemented in the vibroacoustic toolkit. This tool allows us to calculate a reverse projection of the HRTF in a fraction of the time required for the forward projection, saving time and computational overhead. We have tested this algorithm on the CT dataset from a live bottlenose dolphin (acquired from the US Navy Marine Mammal Program). We have also calculated the forward projection of the sound field for use in our model as an alternate validation effort.

Challenges and Solutions: In order to complete the model validation process, we need to acquire a fresh bottlenose dolphin specimen from the NOAA/NMFS stranding network.

RESULTS

Fish Hearing: The Extracted Otolith Simulations produced unexpected results, predicting rocking motions in otoliths exposed to planar harmonic waves from different directions and stimulus frequencies (Schilt *et al.*, 2012). This prediction attracted some attention and sparked discussion in the wider community (Rodgers and Rogers, 2011; Rodgers *et al.*, 2012). Rodgers and Rogers, (2011) suggested that our results, “if true, would have significant implications for our understanding of the mechanisms of hearing in fish.” Subsequently, we created the Simplified Otolith Simulations to test the theoretical basis for the rocking phenomenon. These simulations confirmed the theoretical mechanical underpinnings for the rocking (Krysl *et al.*, 2012). These results are in broad agreement with the work of Rodgers (2011), where the measured transverse (induced-rocking) motion was at about 10% of the longitudinal displacement.

More detail about the Extracted and Simplified Otolith simulations is found below.

Extracted Otoliths Simulations: We collected high-resolution anatomic data from a few small (~21-cm total length) dead *Atractoscion nobilis* (Sciaenidae) from southern California by means of a micro-CT scanner. The scan data was used to extract high-fidelity representations of the otoliths and build a finite element model (FEM) by the methods and tools developed by Krysl et al. (Krysl *et al.*, 2008) and Cranford et al. (Cranford *et al.*, 2008a; Cranford *et al.*, 2008b; Cranford *et al.*, 2008c). This FEM allowed us to investigate the dynamic response of fish otoliths to incident planar acoustic waves whose wavelengths are much longer than the dimensions of the otoliths. The otoliths are modeled as embedded in a shear-soft fluid-like jelly. The simplified model does not currently include any other structures, such as the nearby cranial bones nor influences of the swimbladder. The model space was simulated with two different sinusoidal signals, 200 and 400 Hz (Figure 1), from several different directions with respect to the fish (Schilt *et al.*, 2012).

Shear forces result from the relative motion between the otolith surfaces and the shear-soft jelly that surrounds them in the model space. The results show that the 400-Hz simulation produces greater shear values (due to larger displacements of the otoliths), particularly in the dorsoventral dimension, than does the 200-Hz signal of the same magnitude and direction. Similarly, changing the direction of the acoustic stimulus also produces altered patterns of shear forces acting upon the surfaces of the otoliths. These FEM simulations produced intriguing results, suggesting that frequency and direction may be encoded by the unique rocking motions of the otoliths. If this rocking behavior holds true for actual otoliths within the context of the body, then we will have discovered a basic mechanism for hearing acuity in fish.

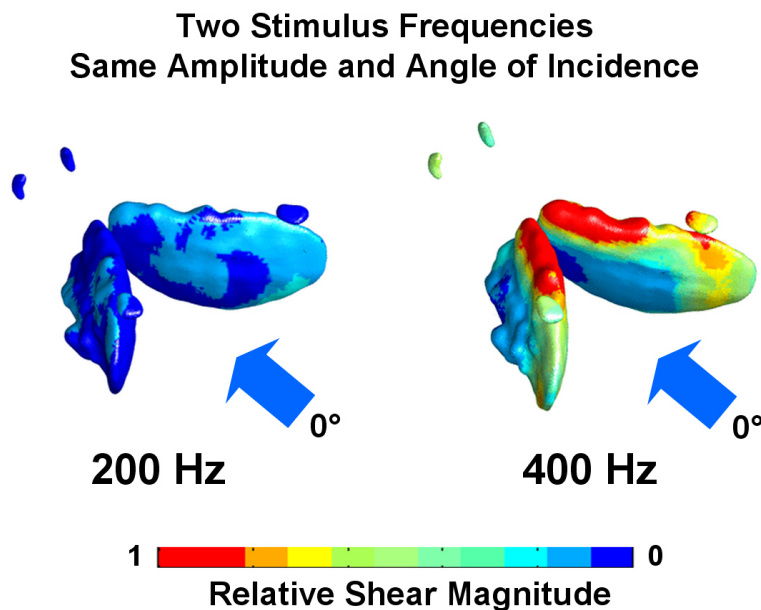


Figure 1: Magnitude of the normalized shear stress over the surface of the otoliths is color-coded. The shear stress may be considered representative of the differential motion of otolith and the soft tissues surrounding it (Schilt *et al.*, 2012).

Simplified Otolith Simulations: The intriguing success of the Extracted Otolith Simulations catalyzed an investigation into whether the simplest “otolith” shapes would produce similar intriguing results. In essence, do some very simple unsymmetrical shapes (scatterers), perhaps the simplest being hemispherical, produce angular oscillations due to torque in the presence of relatively long wavelength acoustic stimuli? These simple scatterers can be considered as “abstractions” of otoliths because they are without the distinctive boat-shape and sculpting found on actual otoliths, features which are often used as keys to species identification. In these Simplified Otoliths Simulations we considered a progressive planar harmonic wave in an acoustic fluid with selected mass density, speed of sound, and frequency.

The acoustic waves impinge upon a stiff homogeneous scatterer (the simplified “otolith”) of arbitrary shape, whose characteristic dimensions are all much smaller than the wavelength of the incident acoustic wave. In the case of a “spherical otolith,” uniform pressure across the symmetrical sphere in the acoustic fluid does *not* generate an accelerating torque on the scatterer. However, the case of the **hemispherical** scatterer is different. There is a dynamic torque experienced by the hemispherical scatterer. The numerical analysis indicates that the X and Z components of the torque are identically zero (these are the directions of the normal to the propagating sound-waves, and the direction of the axis of the symmetry of the scatterer). However, the hemispherical scatterer oscillates (rotationally) about the Y axis (in this direction is parallel to the propagating wave fronts). Indeed, they do rock.

Furthermore, for other non-spherical, *asymmetrical*, shapes, the scattered pressure will generate a dynamic torque which will result in angular motion (rocking) in accordance with the specific parameters and initial conditions (Figure 2). This *principle* suggests that all such “asymmetric” shapes, like otoliths will experience rocking in the presence of relatively long wavelength progressive wave stimuli (Krysl *et al.*, 2012).

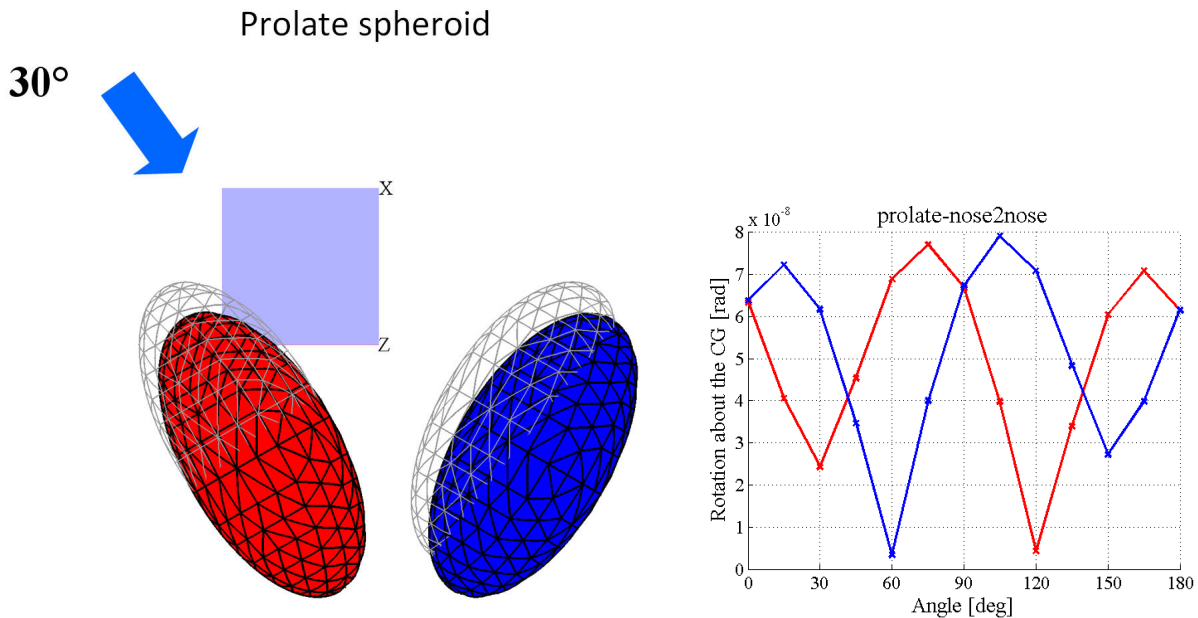


Figure 2: Snapshot from the 3D simulation of the motion of prolate spheroids as synthetic otoliths. The magnitude of the rotation for each scatterer around its center of gravity is a function of incidence angle.

In addition, we have salvaged the sensory maculae from five White Seabass specimens and have obtained a map of the hair cell directions, produced in the laboratory of Dr. Art Popper at the University of Maryland (Figure 3). The impetus here is that if we can combine the fine scale motions of the otoliths from the numerical simulations with the directional map of the hair cells, we may gain clues as to the input to the sensory system and the means by which fish discriminate the frequency and direction of a sound source.

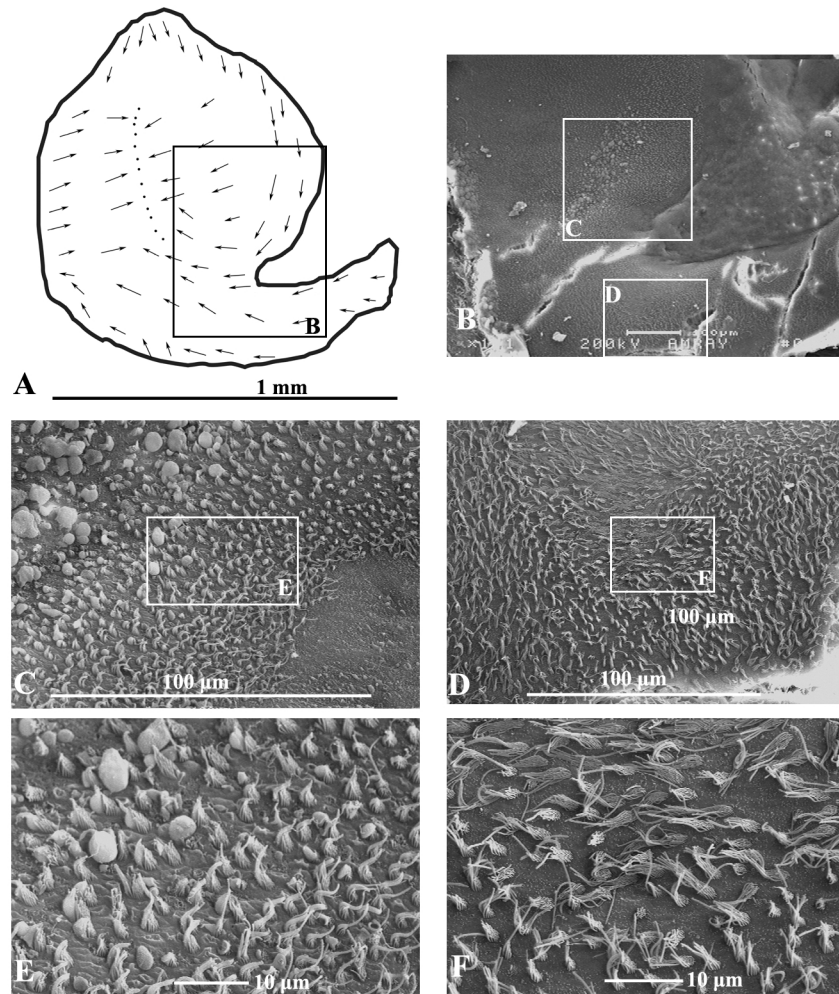


Figure 3a-3f: Scanning electron micrographs (at progressively higher magnifications) of several patches of auditory hair cells (auditory maculae) within the ears of the white seabass (*Atractoscion nobilis*). The maculae underlie the otoliths that, because of their density-related inertia, cause the shear-sensitive hair cells to bend and eventually lead to polarization/depolarization events in the auditory nerve. The longest cilium in each ciliary bundle coincides with the direction of maximum sensitivity to shearing.

Anatomy of Otolith Organs and Sensory Maculae: This is a new capability. The anatomic relationships between the otoliths and the sensory maculae are the basis for the input to the fish central nervous system. Discovering these relationships has been an intractable problem. The extreme hardness of the otoliths and the underlying delicate nervous tissue has prevented serial sectioning. Fortunately, we have found a pre-scan Iodine staining technique developed by Metscher and colleagues (Metscher, 2009a; b) that can reveal the otolith-nerve tissue relationships by CT scanning the prepared specimens (Figure 4).

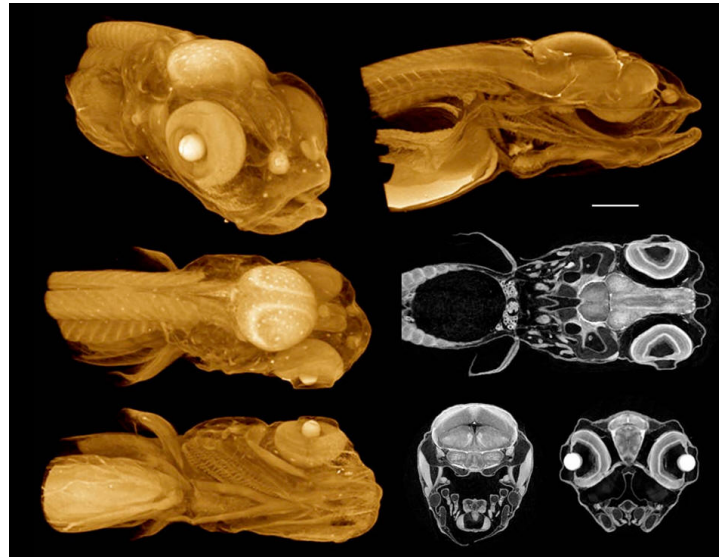


Figure 4: Pike (*Esox lucius*) fry fixed in formalin and stained with IKI. Volume renderings and virtual sections made from the concatenated stacks of reconstructed slices from two microCT scans made with the sample on the same rotation axis (i.e. translated only in the anterior-posterior direction), one scan of the fish's head and the other of the pectoral region. (from Metscher, 2009).

Tissue Elasticity Measurement: Figure 5 shows the prototype of the device based on the concept of the linear skin rheometer. The sample will be located between two plates. The bottom plate is used for support; the top plate has a circular opening that exposes a limited extent of the surface. Force is applied to the exposed surface and the resulting displacement and its phase shift are measured in a certain frequency range. The resulting physical setup is amenable to modeling as the boundary conditions can be estimated with confidence. Also, the sample need not be extracted with high precision.

The data produced by the device will be supplemented by time-of-flight measurements. The combined data set will be subject to computational fitting of the material properties to the measured data. This will allow us to extract simultaneously the bulk and shear modulus of the tissue, and the linear viscosity as the measure of attenuation. All quantities will be functions of the excitation frequency, and could be potentially measured as a function of displacement.

The device will be used to measure properties of tissues during a dissection in the first week of October 2012.

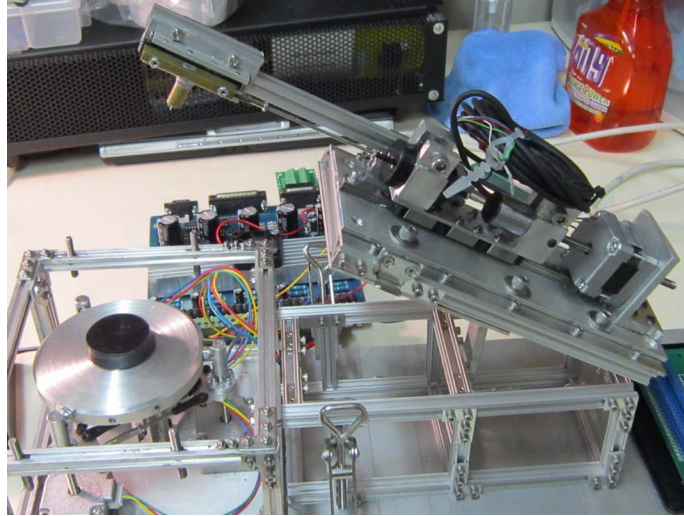


Figure 5: Prototype of the device based on the linear skin rheometer concept.

Model Validation and Dolphin Hearing: The psychoacoustic experiments designed to characterize HRTF in a live bottlenose dolphin are complete (Figure 6). The experimental design calls for us to remain blind to the results until we have constructed and run simulations with an FEM model of a bottlenose dolphin. There has been a delay in obtaining an appropriate specimen. Therefore we will not report the results of the psychoacoustic experiments at this time. Once we obtain an appropriate specimen, we should be able to construct the model in a short time and begin running the requisite simulations.

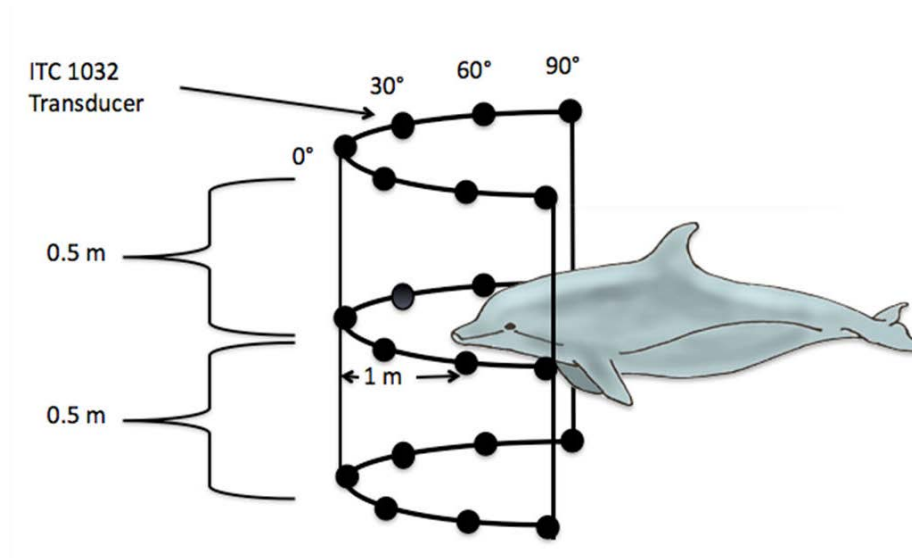


Figure 6: Hydrophone positions for the HRTF experiments.

IMPACT/APPLICATIONS

Fish Hearing: The Extracted Otoliths Simulations and the Simplified Otolith Simulations produced similar “rocking” motions from unsymmetrical “otoliths.” This consistency hints at a potential principle of otolith motion that may be common to all teleosts. We present a hypothesis that otoliths “rock” when exposed to low-frequency sound, and that the collective rocking behavior for the three pairs of otoliths differs as sound frequency and direction changes. This finding has the potential to change our basic understanding of how fish perceive sound.

Future iterations of the model will include additional anatomic components including the otic capsule and tissues that surround the otoliths.

Tissue Elasticity Measurement: The ability to quickly measure elasticity and sound speed in fresh tissue samples will allow us to assess the range of these tissue values across a broad taxonomic spectrum. This is essential to applying the use of these models to other marine and aquatic animal groups with confidence.

Model Validation and Dolphin Hearing: Checking the validity of a finite element model by comparing it to a real world situation is an indispensable threshold to achieve. Once validated, these models and their inherent simulations can be relied upon to provide reasonable approximations for the physical responses of masses and springs in all similarly constructed models. We have already validated our finite element for biosonar beam formation in a bottlenose dolphin and this is a sufficient test of the models. However, before the beam formation tests were complete we devised a validation test based on dolphin hearing by measuring the head-related transfer function (HRTF). When complete, this second test of model validation will provide additional

RELATED PROJECTS

This project is an outgrowth of the innovative methodology we have developed over the past eight years (Soldevilla *et al.*, 2005; Krysl *et al.*, 2006; Krysl *et al.*, 2008; Cranford *et al.*, 2010). We are currently using the same basic methods to study interaction between toothed whale anatomy and selected sounds. In particular, we are studying the processes of sound generation and beam formation. The next big idea is to use the same basic methodology, CT scanning combined with the VATk, to construct a vibroacoustic model for an adult baleen. This project is recently underway, funded by the Office of Naval Research (N00014-12-1-0516), and should allow us to broaden and extend our bioacoustic understanding for some of the world’s largest marine organisms.

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